TUBAIS

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INTERNATIONAL JOURNAL OF
COMPARATIVE
PSYCHOLOGY

Sponsored by the International
Society for Comparative Psychology
and the University of Calabria

VOLUME 4, NUMBER 4

INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

INFLUENCE OF NONOBVIOUS LEARNING ON THE DEVELOPMENT OF THE APPROACH RESPONSE IN CHICKS (*Gallus gallus*)

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ABSTRACT: The role of prenatal auditory stimulations in the development of the postnatal approach response in young nidifugous birds is well known. However most of the studies in this area treat these stimulations as passive events. The purpose of this experimental series is to establish a link between prenatal stimulations and concomitant modifications of embryonic environment (warming and egg turning). Chicks were thus tested in a situation in which they could choose between two pure tones, one of which was or was not prenatally associated with these two stimuli. All chicks of the four groups used here were artificially incubated at the laboratory. After hatching, one-day-old subjects were placed three times a day for 3 days in a situation of choice between two pure tones (HFT = 1000 Hz or LFT = 500 Hz, of 200 ms duration played back every 3 seconds). The operant response (crossing over one of the two active zones in the experimental cage) allows the subject to hear either HFT or LFT. Number and duration of passings over each active zone were recorded. Results of the first control experiment showed that from the first test day naive chicks displayed a spontaneous preference for the low frequency pure tone. Another group of chicks was prenatally stimulated with HFT. This did not significantly affect the initial preference. In a third group, prenatal stimulations were repeatedly associated with modifications of the embryo's environment, i.e., warming and egg rotation. Results showed that the expression of the spontaneous preference for LFT was significantly delayed. The fourth group confirmed the specificity of this effect. The contribution of such nonobvious prenatal learning to the development of the approach response is discussed.

RÉSUMÉ: Le rôle des stimulations auditives prénatales dans le développement des réponses postnatales d'approche des jeunes nidifuges est bien connu. Mais d'une manière générale, ces stimulations sont traitées comme des événements purement passifs. Le but de ces expériences est donc de tester la possibilité d'établir un lien entre les stimulations prénatales et certaines modifications de l'environnement embryonnaire telles que le retournement et le réchauffement de l'oeuf. Des poussins, incubés artificiellement au laboratoire, ont été placés individuellement, trois fois par jour durant trois jours, dans une situation expérimentale leur offrant un choix entre deux sons purs (HFT = 1000 Hz ou LFT = 500 Hz, durée: 200 ms, rythme de présentation: 3 par sec). C'est le passage sur l'une ou l'autre des deux zones actives de la cage expérimentale qui permet au sujet d'obtenir l'audition de ces sons. Le nombre et la durée des passages sur chacune des zones sont enregistrés. Les résultats de l'expérience contrôle montrent que dès le premier jour des poussins "naïfs" s'orientent spontanément vers le son de basse fréquence. La stimulation prénatale avec HFT ne modifie pas de manière significative

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239

ce comportement. Chez un troisième groupe de poussins, HFT a été systématiquement associé avec le réchauffement et le retournement de l'embryon. Dans ces conditions, l'expression de la "préférence" pour LFT est significativement retardée. Un quatrième groupe confirme cet effet en excluant un éventuel effet parasite du nécessaire refroidissement de l'oeuf avant son réchauffement. Ces résultats montrent donc que l'association, au cours de la période prénatale, de stimulations qui ne présentent pas de rapports évidents avec la réponse locomotrice postnatale, modifie cette réponse. La contribution d'un tel apprentissage au développement de la réponse d'approche est discuté.

In young nidifugous birds, the audition of some maternal cries induces behavior such as that of approaching the sound source (maternal assembly call) or, on the contrary, freezing or withdrawal (maternal alarm call). This behavior appears at the appropriate time, just after hatching, is species-specific and appears without previous experience of the object to which the behavior is addressed. It thus seems to be spontaneous or instinctive. A lot of research has shown that, in fact, the development of such behavior is strongly dependant on prenatal audition of their own or sibling vocalizations (Blaich & Miller, 1988; Gottlieb, 1975a,b,c, 1981; Guyomarc'h, 1972, 1973, 1974a,b; Miller & Blaich, 1984).

These studies pointed out the inadequacy of proposing hypotheses in terms of innate or learning mechanisms to explain the ontogeny of "instinctive" behavior and conversely the importance of more subtle forms of experience (Gottlieb, 1982; Miller, 1988; Miller & Blaich, 1984). In actual fact, prenatal auditory stimulation may act either through an effect on nervous maturation (Gottlieb, 1975c) or through familiarization with the frequency modulation of the maternal call (Guyomarc'h, 1972, 1973).

However, this research showing the importance of these prenatal auditory stimulations on the development of behavior that otherwise may be considered spontaneous, treats these stimulations as passive events. Interactions between the embryo and its environment do exist before hatching. For example, Tuculescu and Griswold (1983) have shown that vocal interactions between the embryos and the hen take place during the prehatching period.

In fact, maternal vocalizations are frequently produced at relevant times of the embryo's life (e.g., when the mother comes back to the nest or during postural changes (Guyomarc'h, 1974b). These vocalizations thus may be associated with some pertinent events such as warming or egg rotation that provide many stimulations and that are important and necessary to ensure correct embryo development. Such interactions taking place necessarily in the embryo's natural environment are generally not taken into account. They are even reduced or purposely suppressed to control experimental factors.

The purpose of this study is to examine the effect of prenatal stimulation in an experimental context closer to that existing in natural conditions. In particular, these experiments have been designed to test effects of the association of embryo environmental modifi-

cations (such as warming and egg rotation) with auditory stimulations.

GENERAL METHODS

Subjects

The subjects were 67 domestic chicks (*Gallus gallus*). Fertile eggs were obtained from a single supplier and incubated at the laboratory. The type of incubator used (Favor 2 incubator) did not include a fan or automatic egg rotation. This was always done manually. Moreover, the incubator was placed in a sound-attenuated room so that external artificial noise interference could be controlled.

Subjects were assigned to four groups according to the prehatching treatment (no stimulation: n = 15; auditory stimulation: n = 15; auditory stimulation paired with warming and egg rotation: n = 19; cooling: n = 18). Subjects of each group were kept together in breeding cages (60 cm × 60 cm × 120 cm) in a room continuously warm (28°C). Food and water were available *ad libitum*.

Apparatus and Test Situation

After they had been taken out of the incubator, chicks were tested for the first time at 20 hours of age (+/− 4 hours). Prior to testing, subjects were marked on the top of their heads with a marking pen for rapid and easy identification.

Experiments were run in a testing cage (40 cm × 40 cm × 40 cm), and 128 photocells set regularly (.62 cm apart) along two adjacent sides of the cage (64 on each side) enabled us to follow the chick's movements. The vertical position of photocells was adjusted so that the chick remained at all times within the beam. The mean of the chick's positions, computed once a second by microprocessor (Apple IIe), was displayed on a monitor.

Two "active" zones close to opposite walls (40 cm × 12.4 cm = 64 × 20 photocells) were marked out by stripes on the floor of the cage. The operant response, passing over these zones, triggered auditory stimuli which were presented for a maximum of 20 seconds. Stimuli were presented again only if subjects recrossed into active zones. Loudspeakers were placed in front of the zones.

Auditory Stimulus

Two pure tones of 200 milliseconds duration were used as test stimuli : a high frequency tone (HFT = 1000 Hz) and a low frequency tone (LFT = 500 Hz). These artificial stimuli were preferred to natu-

ral specific vocalizations for two reasons. First, as chicks were incubated together they could hear other embryos (and themselves). The effects of noncontrolled pairing of the embryo's vocalizations with external events were avoided with the use of pure tones. Second, specific vocalizations (maternal or sibling calls) may contain some components which spontaneously trigger off behavioral responses. Despite being in the maternal call frequency range, the pure tones did not contain other obvious normal features (duration, rhythm or frequency modulation) proved by research to be crucial to specific recognition (Collias & Joos, 1953; Guyomarc'h, 1974b; Gottlieb, 1978, 1982; Guyomarc'h, Gardahaut & Fenaux, 1982; Gaioni & Evans, 1985; Collias, 1987).

HFT and LFT were recorded on a tape loop of 90 seconds duration (one tone per track) and broadcast from a Revox A77. All tape loop auditory characteristics, except frequency, were the same for HFT and LFT (rhythm : one tone every three seconds; intensity: from 75 to 80 dB, depending on the position in the cage). Sound level was measured with a Brüel and Kjaer (type 2226).

HFT was also used as the prenatal auditory stimulus for two groups of subjects.

Test Procedure

Subjects used in the four experiments of this series were individually tested three times a day for 3 days, that is to say nine sessions in all. At the first three daily sessions, their ages were 20, 44 and 68 hours ($+/-$ 4 hours). At the beginning of each experimental session, the subject was placed at the centre of the experimental cage. Each experimental session lasted 15 minutes. To minimize the effects of cyclical variation of activity, the experimental sessions took place at different times of the day with 3 hours ($+/-$ ½ hour) between two consecutive sessions.

In order to test for possible positional biases, the active zones were reversed for each half of each group of subjects. The subject was returned to its breeding cage at the end of each session.

Number and duration of passings recorded over the two zones (Z1 = LFT and Z2 = HFT) were pooled into blocks (B1, B2, B3) of three consecutive sessions and compared (Z1 versus Z2).

Analyses of variance (VAR.3, Lepine, Rouanet & Lebeaux, 1976) were performed on the following factors: subjects, zones, sessions, blocks of three sessions.

EXPERIMENT 1 : SPONTANEOUS CHOICE BETWEEN TWO PURE TONES

This first control experiment was designed to test for initial preference for either of these tones.
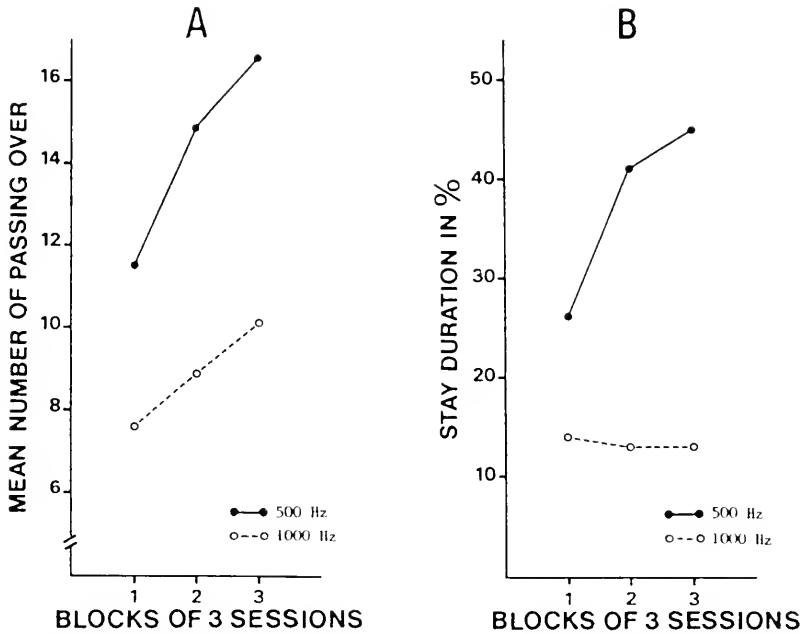
FIGURE 1. Spontaneous choice between two pure tones. Graphs
show (A) numbers of passing over each zone totalized across all sub-
jects in each block of three sessions and (B) mean stay duration by
chick for each block of three sessions.

Method

Fifteen experimentally naive chicks were used in this experi-
ment. Crossing into one zone triggered the LFT ; crossing into the
second one triggered the HFT.

Results and Discussion

From the very first block of three sessions (B1), chicks oriented
towards the zone associated with the low frequency tone (Figure 1).
Stay duration in this zone was significantly higher than in the other
one, for all three blocks of three sessions (B1 : $F(1,14) = 11.56$; $p<.01$;
B2 : $F(1,14) = 16.98$; $p<.01$; B3 : $F(1,14) = 32.63$; $p<.01$). The same
pattern was recorded for the numbers of passings over (B1 : $F(1,14) =$
6.49 ; $p<.05$; B2 : $F(1,14) = 29.80$; $p<.01$; B3: $F(1,14) = 28.56$;
$p<.01$).

Chicks having no acoustic experience with either of these two
tones showed a clear-cut preference for the low frequency tone. This is
in agreement with the data obtained by Fischer (1972) but the rea-
sons for such a preference are not obvious. One possible explanation

is, as Gray (1990) and Gray and Rubel (1981, 1985) have shown, that the newborn chick's response threshold to high frequency pure tones is higher than to low frequency ones. This greater sensitivity might thus explain the precocial preference for LFT. However it must be noted that, for each block, the subjects always stayed more than 10% of the time on the HFT one; this provided them with several opportunities to perceive HFT. The persisting preference for LFT cannot therefore be due only to the precocity of the highest sensitivity to low frequencies.

Another nonexclusive explanation may then be proposed. Gray and Jahrsdoerfer (1986) have shown that naturalistic sounds elicit more consistent and more sensitive responses than more arbitrary ones. In the present study, LFT did correspond to one of the maternal call frequencies. According to Guyomarc'h (1974b) maximum maternal call energy is concentrated on this frequency. Thus, experimentally isolated chicks, without any other perceptual feature to allow identification, may seek the perception of this frequency belonging to the maternal repertoire.

EXPERIMENT 2 : EFFECT OF PRENATAL STIMULATIONS

Experiment 1 had shown that the high frequency tone is less attractive than the low frequency tone. This study was designed to test the effect of prenatal stimulations with HFT on the chick's postnatal behavior.

Method

Fifteen chicks were used in this experiment. Konishi (1973) has shown that the auditory system is functional at 18 days of incubation. Thus, during the last 3 days of incubation (from day 18 to day 21), embryos were stimulated with HFT twice per day, for 15 minutes (rhythm : one tone every 3 seconds; intensity: 75 dB). In all, they thus received six periods of stimulation. No obvious embryo environmental modification was paired with auditory (HFT) stimulations. In particular, manual egg rotation took place outside the auditory stimulation periods.

Except for these prenatal stimulations, the procedure was the same as in the previous experiment.

Results and Discussion

Figure 2 shows results obtained in this condition. As in experiment 1, chicks clearly oriented towards the zone triggering the low frequency tone and always stayed longer in this zone (B1: $F(1,14) =$
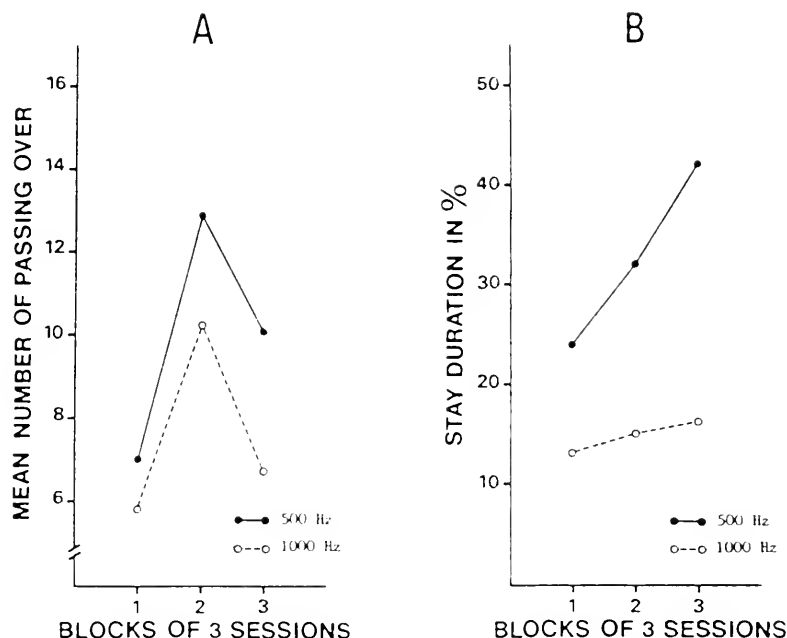
FIGURE 2. Effect of prenatal auditory stimulations with the high-frequency tone.

6.50 ; p<.05; B2: $F_{(1,14)}$ = 5.63; p<.05 ; B3 : $F_{(1,14)}$ = 16.56 ; p<.01). The same tendency is noted for the number of passings over. From the very first experimental session, chicks passed over the LFT zone more frequently ($F_{(1,14)}$ = 10.35, p < .01). Nevertheless, the difference did not reach a significant level when computed for the three sessions of B1 ($F_{(1,14)}$ = 2.93 ; NS). During the two other blocks, chicks crossed over the LFT zone significantly more often (B2 : $F_{(1,14)}$ = 4.99 ; p<.05; B3 : $F_{(1,14)}$ = 19.44 ; p<.01).

Thus, chicks that had been prenatally stimulated with HFT did not behave in an obviously different manner from experimentally naive chicks.

EXPERIMENT 3 : PRENATAL STIMULATIONS ASSOCIATED WITH ENVIRONMENTAL MODIFICATION

The purpose of this experiment was to test the effect of prenatal stimulations which had been paired with warming and egg rotation.

Method

Nineteen chicks were stimulated prenatally. During the last three days of incubation, eggs were taken out of the incubator, twice
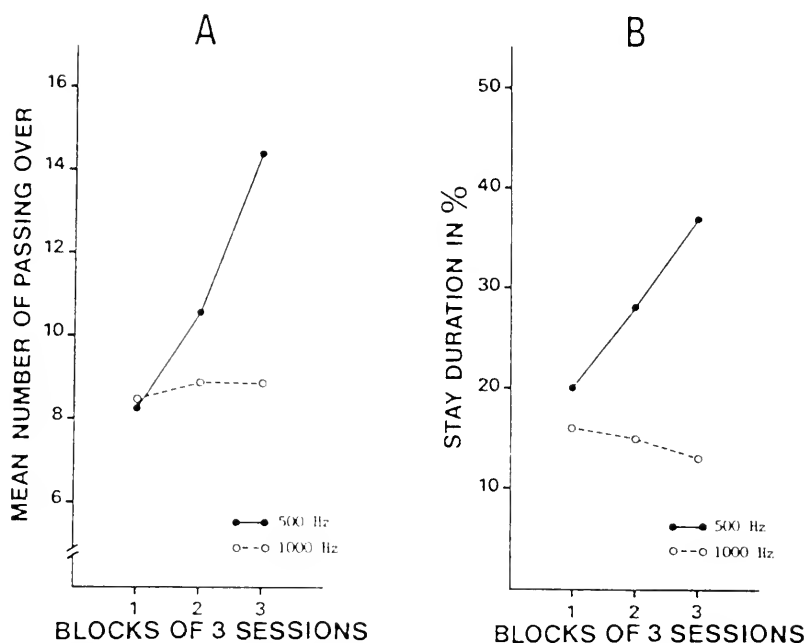
FIGURE 3. Effect of prenatal auditory stimulations with the high frequency tone repeatedly associated with environmental modifications.

a day, for fifteen minutes. They were turned over just before being put back in the incubator and then stimulated with HFT for fifteen minutes. The high frequency tone was thus associated both with the turning over and the warming. As in the previous experiment, embryos received six periods of prenatal stimulation ; the testing procedure was not modified. In this way, chicks were submitted both to a Pavlovian conditioning paradigm and to an operant conditioning paradigm.

Results and Discussion

The results obtained during this experiment are clearly different from those recorded in the preceeding experiments (Figure 3). Times spent in the two zones were not significantly different during the first block (B1 : $F(1,18) = 0.60$; NS). Subjects stayed significantly longer on the LFT zone only during the last two blocks (B2 : $F(1,18) = 7.47$; $p<.05$; B3 : $F(1,18) = 30.98$; $p<.01$.

Again, during the first two blocks of sessions, the numbers of passings over the two zones were not significantly different (B1 : $F(1,18) = 0.05$; NS ; B2 : $F(1,18) = 2.05$; NS). But, activity signifi-

cantly increased on the zone which allowed audition of the low frequency tone between the second and the last blocks ($F(1,18) = 4.58$; $p<.05$) and, during B3, the difference between the two zones reached a significant level ($F(1,18) = 6.75$; $p<.05$).

The choice of the lower frequency tone was then noticeably delayed and a significant difference for the two criterions appeared only during the last block of sessions (third day of experiment).

These results showed that the experimental procedure used here modified the postnatal behaviour of chicks in a significant manner. This effect was confirmed when the difference between the numbers of crossings over the two zones during experiment 1 (naïve chicks): DE1 was compared with the difference between the numbers of crossings over the two zones during experiment 3 (warming and egg rotation paired with HFT): DE3. DE1 appeared significantly higher than DE3 for the first two blocks of sessions (B1: $F(1,32) = 5.50$; $p<.05$; B2: $F(1,32) = 7.01$; $p<.05$).

It is of interest to recall that, in the first block (B1) of experiment 2, the difference between the numbers of passings over the two zones did not reach significant level. A comparison between DE1 and DE2 (experiment 2) was thus made for B1. DE2 did not appear significantly different from DE1 ($F(1,28) = 2,38$; NS). This lack of significant difference tends to indirectly confirm the fact that prenatal stimulation alone is not the main determinant factor.

EXPERIMENT 4: EFFECT OF COOLING

Results of experiment 3 seem to point to an effect on the postnatal auditory preference due to the prenatal audition of HFT being associated with warming and egg rotation. Nevertheless, another interpretation may be proposed. Indeed, during this final experiment, eggs were taken off the incubator six times and were thus cooled six times.

Thus, the time lag noted in these conditions may be due to a general effect from cooling. The present experiment was designed to test this hypothesis.

Method

Eighteen chicks were used in this experiment. As previously, during the last 3 days of incubation, eggs were taken off the incubator, twice a day, for 15 minutes. They were turned over just before being put back on to the incubator but were not stimulated with any sound. Testing procedure was not modified.
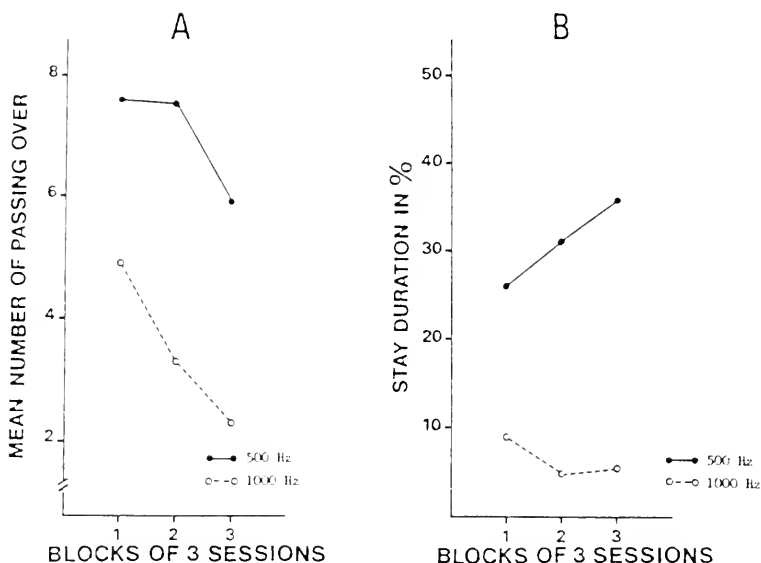
FIGURE 4. Effect of cooling on the postnatal choice.

Results and Discussion

As in experiment 1, chicks oriented towards the LFT zone (Figure 4). All differences were significant for both duration (B1: $F(1,17)$ = 27.11; p<.01; B2: $F(1,17)$ = 42.36; p<.01; B3: $F(1,17)$ = 55.65; p<.01) and numbers of passings over (B1: $F(1,17)$ = 35.82; p<.01; B2: $F(1,17)$ = 30.30; p<.01; B3: $F(1,17)$ = 42.70; p<.01).

Thus, cooling appeared to have no effect on the spontaneous preference for LFT after hatching. The time lag recorded in experiment 3 may thus be interpreted as a specific effect of the association of prenatal auditory stimulation with warming and egg rotation.

GENERAL DISCUSSION

The results presented here show naive chicks, placed in an experimental situation of choice between two pure tones, spontaneously preferring the low frequency one.

Such a preference was to be expected since it is well known that sensitivity to low frequencies matures earlier (Konishi, 1973). Saunders, Gates and Coles (1974) have also shown that there is a peak sensitivity at 800 Hz. Moreover, according to Fischer (1972) low frequency pure tones are more attractive than high-frequency ones and data obtained by Gray and Rubel (1981) indicate that low frequency

tones (in the range of their maternal assembly call) suppress more effectively distress vocalizations in one-day-old chicks than the high frequency tones.

This is consistent with previous data which emphasized the role of low frequencies in the attractiveness of the maternal call (see for example Gottlieb, 1975a,b). It must be noted that although this preference is strong right from the first day (except in experiment 3), it nevertheless increases later on. Thus, neither the effect of age nor of familiarization with HFT were present.

So, even if the greater sensitivity for low frequency tones may partly explain the precocial spontaneous preference, its persistance throughout the experiment indicates that the chick's locomotor response is unconditionally orientated towards LFT.

Passive prenatal experience with HFT (experiment 2) did not impede the spontaneous preference for the low frequency tone and the chicks' postnatal behaviour was not significantly modified. Thus, in these experimental conditions, prenatal auditory stimulation with a nonspecific tone has no obvious effect. It may be hypothesized that, in natural conditions, this contributes to the embryo's "protection" against environmental, not pertinent, auditory stimuli and allows the neonate to avoid postnatal "errors."

Conversely, results of the third experiment showed that repeated prenatal association of HFT with pertinent environmental modifications (warming and egg rotation) significantly delayed the postnatal choice of the low frequency tone. As shown by experiment 4, this effect was not due to a general effect of the cooling which occurred just before warming.

These results are important. Indeed, they show that postnatal locomotor responses are partly dependant upon events occurring during the late embryogenesis and they support the view which stresses the continuity between prenatal and postnatal behavior (Schneirla, 1965; Bekoff, 1981).

Moreover, auditory stimulations as well as warming or egg rotation did not present any characteristic which may be obviously linked to the development of a locomotor response. Nevertheless, prenatal pairing of these two types of stimulations has modified the postnatal approach response. Thus, nonobvious prenatal learning must be taken into account when studying the development of social attachment.

As stated above, the maternal call attractiveness is generally used to test and quantify preferences for certain vocalizations or for some physical characteristics of such vocalizations. Data presented here provide us indirectly with the elements for making hypotheses to explain the origin of this attractiveness.

Indeed, everything we have discussed so far points to the importance of prenatal stimulations. In natural conditions, embryos can

hear maternal calls. These calls are likely to be associated in some cases with modifications of the embryo's environment such as warming and egg rotation. This process may, likely, favor postnatal responses to specific stimuli. Nevertheless, it must be noted that siblings' calls may also be associated with some of these modifications. Furthermore, their importance in the development of responsiveness to maternal assembly and alarm calls is well known (Gottlieb, 1981; Blaich & Miller, 1988). In particular, prenatal audition of these calls facilitates the development of high frequency sensitivity and maintains repetition rate specificity (Gottlieb, 1975a,b,c,1979). Maternal and siblings calls may thus "compete" after hatching. The marked spontaneous preference for low frequency which is part of the maternal repertoire is likely to contribute to setting normal attachment to the hen.

But prenatal learning also contributes to adjusting the postnatal approach response. Indeed, after repeated pairing with some pertinent prenatal events, auditory stimuli, including maternal vocalizations in particular, could became secondary reinforcers. Thus, after hatching, chicks may seek the best perception of these stimulations and to do so, approach the sound source.

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BEHAVIOURAL SCREENING AND SELECTION THROUGH AFFINITY: THE CASE OF POLYGYNY IN PAPER WASPS (*Polistes dominulus*)

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ABSTRACT: An evolutionary model for emergence of polygynous foundation in polistine paperwasps is proposed. Adapted from Hamilton's model, the model is based on selection through affinity, a process of genetic assortment. This would involve selective association of founding wasps on the basis of common possession of a behavioural trait. The model, therefore, invokes a form of behavioural screening in a genetically heterogeneous population. The validity of the hypothesis and the nature of the trait concerned are considered in relation to observations on formation of Polistine polygynous associations and between species comparisons.

RÉSUMÉ: On propose un modèle évolutif de l'apparition de la fondation polygyne chez les Polistes. Placé dans le cadre du modèle général de Hamilton, ce modèle, appelé sélection d'affinité invoque un processus actif d'assortiment génétique. Il repose sur un postulat, taxé de postulat d'affinité, selon lequel la réalisation d'une fondation polygyne ne peut se faire que si tous les sujets ont acquis un même trait de comportement qui n'existe pas dans les espèces strictement monogynes. On examine la vraisemblance de ce postulat et on cherche a déterminer la nature de ce trait commun par étude comparée du comportement dans plusieurs espèces.

> "It is always difficult to draw unambiguous distinctions in
> Biology, but it is often valuable to try"
> > Maynard Smith, J. (1976).

INTRODUCTION

The origin of a sterile caste in Hymenoptera societies is most frequently explained by means of the model of Hamilton (1964). More generally speaking, the concept of inclusive fitness, basic for the model, allowed many authors to account for altruistic behaviour in social Hymenoptera despite its apparent selective disadvantage (West-Eberhard, 1969, 1978; Jeanne, 1980; Gadagkar, 1985a, b; Ito, 1987);

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253

some of these forms can represent steps in the progression of the sociality in the evolutionary process in Hymenoptera.

In Hamilton's model, selection for an altruistic behavioural trait depends on the degree of genetic similarity between helper and helped, in terms of the gene responsible for that trait. Thus, this model has sometimes been called a model of genetic relatedness (Pamilo, 1984) or of genetic similarity (Rushton, Russell, & Wells, 1984; Rushton & Nicholson, 1988; Parker 1989).

In nature, pedigree relatedness is indeed the simplest explanation for genetic similarity between individuals. Thus Hamilton's model uses Wright's coefficient of relationship r, a quantitative measure of pedigree relatedness, to measure the degree of genetic relatedness. That means that pedigree relatedness was implicitly considered by most authors as the only determinant of any genetic similarity between helper and helped. For that, the model of Hamilton was often considered as a model of kin selection (Maynard Smith, 1964).

In fact, pedigree relatedness is not the only reason why helper and helped animals can be genetically similar. Dawkins (1976) pointed to a possible model (known as the "green beard" model), by which such a similarity would result from the existence of a clearly recognizable cue (such as a green beard) bound to the possession of the altruistic gene. Thus, any altruistic animal would be allowed to specifically help genetically similar subjects by turning its cooperative behaviour towards other animals possessing a green beard. Nevertheless, this author did not believe that such a model, less economical than the kin selection model, could have a noticeable extension.

Indeed, it meets an objection, proposed by Maynard Smith (1976), claiming that any genetic similarity between helper and helped animals for other reasons than pedigree relatedness is less likely a priori. This is because the evolutionary process would have implied simultaneous adoption of altruistic behaviour per se and active preference for genetic relatives as the beneficiaries (having a green beard in the case stated by Dawkins). In contrast, the classic kin selection model seems to be more simple and more likely.

The point is that, in these models, altruistic behaviour and choice of the helped animal are considered as being distinct traits of behaviour: there is a trend in evolutionary ethology to consider any trait that can be distinguished by observation as related to a distinct unit of selection.

This assumption is not necessary; any interactive behaviour within a population can change the conditions of selection. At a theoretical level, Eshel and Cavalli Sforza (1982) showed that "structural assortment" during association could substitute for kin selection and account for cooperation.

In previous papers (Pratte & Gervet, 1980; Gervet, 1986) we

claimed that association of females may result from behavioural screening during the establishment of a society, so that only individuals carrying the behavioural trait under selection can indeed associate. Members of these societies will then be genetically similar, but this will not be because of genealogical relatedness. A process of this kind has been called selection through affinity or "pal" selection; we consider as "pals" individuals that tend to associate together on the basis of common possession of a same behavioural trait.

In the present paper we discuss the possible evolutionary emergence of Polistine polygynous societies in this theoretical context.

POLISTINE POLYGYNY

In some Polistine species, several foundresses may associate to form a polygynous society (Pardi, 1942). It is well known that this is followed by behavioural differentiation, one individual becoming specialised as the main egg-layer, while others, the auxiliaries, either suspend laying, or their eggs are destroyed by the main layer (differential oophagy, Gervet, 1964 b).

Such societies are interesting for students of evolution for two reasons. First, this condition may illustrate a stage along the evolutionary route to semi-sociality (Lin & Michener, 1972), or to eusociality in insects. In fact, it has been stated (Ross & Carpenter, 1991) that the situation of polygynous Polistes does not represent a remaining ancestral situation but only a selective response to peculiar ecological circumstances, which is compatible with structural constraints present in the Polistine. But West-Eberhardt (1978) suggested that selection acting on behaviour expressed by members of polygynous societies could be similar to that which had led to primitive sociality, with its incipient interindividual behavioural differences. Second, polygynous societies raise the general problem of altruistic behaviour. How can there have been selection for the auxiliary or helper condition, which would seem to imply a lowered fitness?

In answer to that question, West (1967, West-Eberhard, 1969) proposed a model inspired by Hamilton (1964).

West (1967) showed that a female will "benefit" from joining a founder as an auxiliary, and in ceasing laying in the resulting digynous society, if the condition:

$(P_{(f+j)} - P_{(f)}) / P_{(j)} > 1/r$ is satisfied, where:

$P_{(f)}$ = productivity of the founder (if it were to remain solitary)

$P_{(f+j)}$ = productivity of the digynous colony in founder's offspring

$P_{(j)}$ = joiner's productivity had it reproduced alone

r = coefficient of relationship (fraction of shared genes) between the founder and the joiner.

These conditions are quite strict, but, according to West, could be satisfied by the combination of three conditions:

First, productivity of the polygynous group is significantly greater than that of a solitary founder;
Second, the joiner's own productivity is low, so that it loses only a small number of descendants in return for a surplus ensured through the founder's increased production with the aid of the joiner;
Third, associated wasps are closely related.

The first condition is the most easily satisfied: the dominant member lays more eggs than if it were solitary and most of the eggs laid by auxiliaries are destroyed by differential oophagy (Gervet, 1962, 1964), the colony is more resistant to destruction (Gibo, 1978), predation (Ito, 1986), and usurpation (Gamboa, 1978). It also exploits the habitat more efficiently (Gamboa, 1980). It may be that the main advantage of polygyny is more closely related to increased chances of nest survival than to any increase in daily laying. In other words, the important feature is not the increase in egg-laying as such, but the improved survival of colonies, which naturally results in greater overall egg production. If so, any such advantage would be closely linked to local ecological conditions such as prey or predator abundance. These in turn could depend on latitude (Jeanne, 1979).

If monogynous founding has only a very low probability of producing offspring, an advantage to polygyny will persist, even when colony-member kinship is low. Hence, predictions of kin and individual selection models will no longer differ whenever a subordinate has any probability at all of replacing an alpha as main-layer (Queller, 1989).

Intrinsically lower fecundity of wasps which assume auxiliary status is less certain. Social relationships established between wasps meeting for the first time do reflect fairly accurately their respective laying rates (Gervet, 1964) and endocrine states (Röseler, Röseler, & Strambi, 1980; Röseler, Röseler, Strambi, & Augier, 1984; Röseler et al., 1986). But, such directly detectable physiological traits do not seem to be of much value as measures of their potential fecundities.

Finally, measures of the degree of kinship between nest companions vary. They are sometimes such that they could confer a genetic

advantage on the helper (Metcalf & Whitt, 1977). However, more extensive studies have often shown that these relationships may often be no closer than a wasp would have had with its own offspring (Queller, Strassmann, & Hugues, 1988; Strassmann et al., 1989). Where this is so, there would be no selective advantage to polygyny, unless benefit in terms of offspring produced were to exceed largely the costs of polygyny. On the other hand, any factor which significantly reduced adult life-span (or life-expectancy of a monogynous nest) would increase the selective value of association, even when members' coefficients of relatedness were low. Even in the most northerly regions, levels of monogynous colony failure during pre-emergence can be very high, including that for strictly monogynous species (Yamane, 1969).

Preferential association is usually accounted for in terms of kin recognition, itself implying that responses of individuals to others are a function of degree of genetic relatedness (Byers & Bekoff, 1986). There is evidence that genetically dependent chemical odours (in relation to environmental factors) could mediate such recognition and distinction in wasps (Gamboa, 1988). This has also been indicated for other species (see Gadagkar, 1985b, for review). Nevertheless, Grafen (1990), has pointed out that appreciable assortment of interacting individuals is not, by itself, a conclusive argument in favour of kin selection.

At present, then, kin selection, based on West's model can account for Polistine polygyny. However, in several instances, it is necessary to invoke supplementary hypotheses, however reasonable they may be, for this to be so. In some ecological conditions, West's model constitutes a reasonable hypothesis. Yet this does not contradict the occurrence of other mechanisms. In Ito's (1986) words, " . . . mutualism, manipulation and kin selection may all have contributed to the evolution of eusociality in the Hymenoptera."

However, we believe that another question deserves as much attention as the more detailed study of environmental conditions which each species encounters. This concerns definition of the point at which natural selection actually acts, i.e., the identity and nature of the trait affected. When West asks "what is the selective advantage to join a colony as an auxiliary?" the question implies a prerequisite: the relevant selective process would have consisted of the change from a wasp that founds for itself to an auxiliary. It seemed to us that the first prerequisite was to ask "what is, in fact, the basic difference between species which respectively do and do not found polygynous societies?" To answer this question, we tried to analyse the behaviour of females belonging to a species that practise polygynous foundation and compare it to that of other species.

EMERGENCE OF A POLYGYNOUS SOCIETY: THE EXAMPLE OF
Polistes dominulus

In laboratory conditions, we observed the successive steps that lead to the formation of a polygynous society after putting two foundresses in the same cage. A flow chart (Figure 1) summarises these events. Bifurcations show where alternative responses are possible, but only one leads directly to a polygynous society.

When two wasps meet, they may turn aside and separate, with no further development of contact, though they may meet again later. This can happen under natural conditions when two wasps encounter one another in a noncompetitive situation, or at a drinking point. Absence of any further interaction is seen only between two captive *Polistes dominulus* females which have never met before, if their activity level is low. If contacts develop further after meeting (first branch point), antennal displays, described in various previous studies (Pardi, 1946, 1948; Gervet, 1964a), follow. When two or more *P. dominulus* females are placed in the same observation cage, they invariably engage in this type of interaction. Each wasp beats the foreparts of the other with its antennae, with accelerating intensity. This process may be interrupted at any moment; the wasps then separate. In an experimental nest-box, no wasp can flee far away and soon, both females encounter each other again.

When interactions of this kind are prolonged, there are two possible outcomes (the second branch-point). If such individual display patterns are maintained by both individuals (i.e., the interaction remains symmetrical), they graduate to overt aggression. A violent combat ensues, which may result in death of one of the wasps. This progression may again be interrupted at any stage by separation, whether because one or the other takes flight, or due to a disturbance. Alternatively, differences in individual behaviour may appear. One of the wasps ceases antennal beating, lowers the head and antennae, and adopts a characteristic (acinetic) posture, while the other continues its antennal beating. The asymmetry is stable, persisting over any number of subsequent encounters between the same individuals. The intensity of the interaction may, however, wane with time. The antennal and associated movements may become scarcely perceptible, even though a fundamental asymmetry in the response persists.

Such stable differences between individuals at the outcome of a fight, which may have involved no more than a slight preliminary interaction, come under the classical definition of social dominance. The fight that results can be described as a differentiation contest (Yoshikawa, 1956).

Emergence of a dominance relationship between two foundresses in reproductive condition, and ultimately the decrease in aggressive
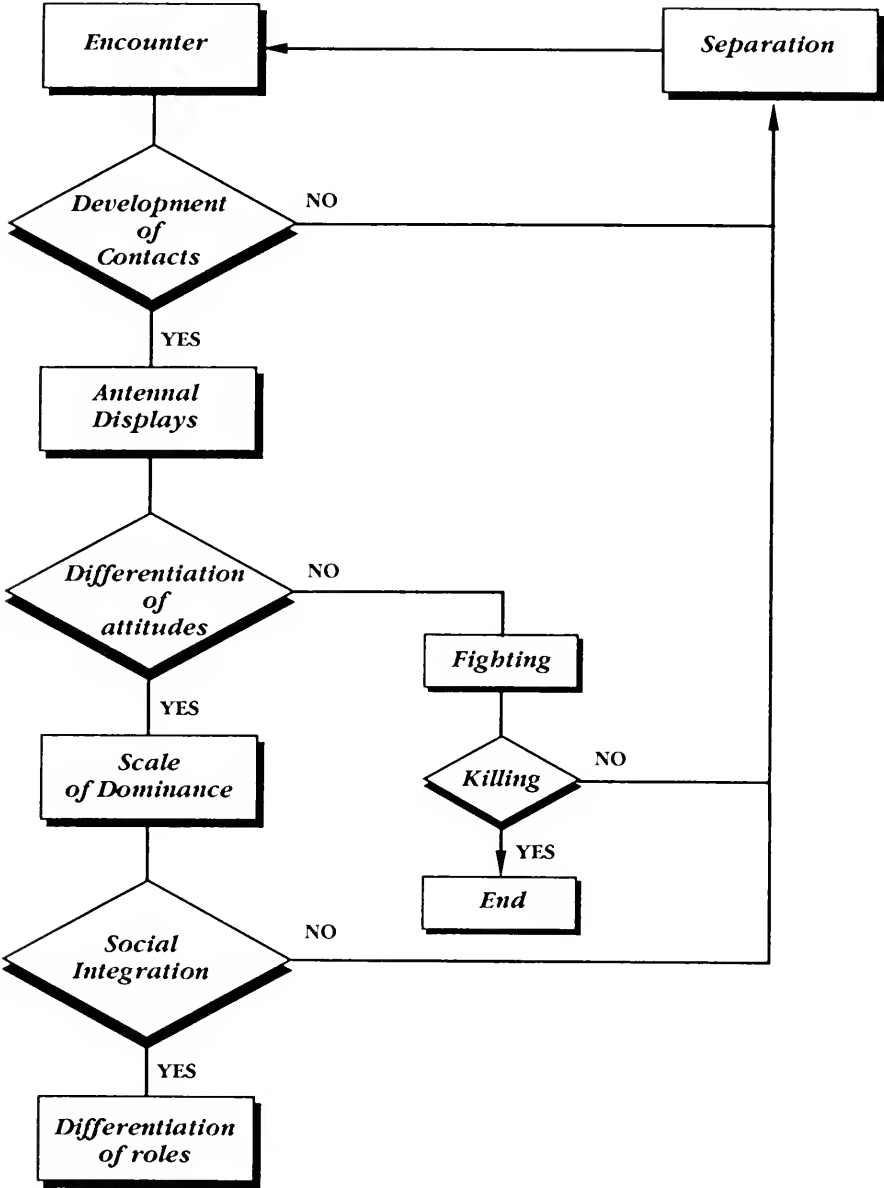
FIGURE 1. Succession of events during the formation of a poly-gynous society.

interactions which results are alone not enough to ensure their integration in a digynous society. Two alternatives may then be open (the third branch-point):

In species where polygynous foundation does not exist, the subordinate is attacked or moves away whenever it attempts to return to the nest, even if it adopts subordinate behaviour. If it is the original foundress which assumes subordinance, this is called usurpation (Yoshikawa, 1955). Such species are said to be strictly monogynous.

In species which do polygynous foundation, like *P. dominulus*, the two wasps can continue to cohabit. They adopt their complementary behavioural attitudes with progressively decreasing intensity in later encounters. Then, but only then, can social integration be said to exist. Such species are said to be potentially polygynous.

In this last instance, hierarchical differentiation is followed by a difference in reproductive activity, and in the expression of other activities. The polygynous society is then said to be functionally monogynous. The same kind of differentiation seems to occur in all Polistine species during polygynous foundation which have been studied so far, concerning laying, differential oophagy and contribution to social tasks. Thus, the difference between the two kinds of species does not concern the existence of a differentiation fight nor the subsequent existence of a stable differentiation of attitudes but the consequences of such a differentiation.

In a strictly monogynous species, fights of this kind occur particularly when a foundress regains a nest already occupied by another foundress. At the end of such a fight (of variable degree of violence) protagonists may adopt complementary dominant and subordinate postures, unless one individual previously abandons the nest (Yoshikawa, 1955; Kasuya, 1981; Makino & Aoki, 1982). Departure of the wasp which has "lost" the fight (and which has adopted a submissive or acinetic posture) is the most evident outcome. The behavioural difference resulting from combat supresses attraction of one individual to the nest occupied by the other. The latter continues to harrass, if not aggress, any foundress that comes to the nest, even if it adopts a submissive posture.

Potentially polygynous species do not differ fundamentally from strictly monogynous species, either in intrinsic tendency to join an already occupied nest, or engaging in a combat at the nest, which will lead to differentiation. Two traits which involve a certain ritualization of social contacts do, however, allow the two categories to be distinguished:

When a wasp of a polygynous species becomes subordinate, its attraction to the nest does not disappear, and it remains on the comb, adopting a submissive posture at any encounter with the dominant companion. A more detailed study has shown lower nest presence, but

more particularly, that the behaviour of the subordinate is different (Pratte, 1990a, b). Response to social stimulation is modified after establishment of a hierarchy, with increased responsiveness to larvae and reduced egg-laying (Röseler et al. 1984, 1986), and differential oophagy (Gervet, 1964b).

A wasp which becomes dominant usually ceases to aggress its protagonist as soon as the latter adopts a submissive (acinetic) posture. Its dominance is then expressed in a calmer, more ritualized expression of its initial aggressiveness. Correlated behavioural modifications (increased laying, prolonged nest occupation) also indicate that there are other differences in the behavioural responses related to the nest comb. The events shown in Figure 2 outline the interactions and the assumption of different behavioural roles by the individuals concerned, for strictly monogynous and potentially polygynous species respectively.

We stress here that the difference between the two kinds of species simultaneously involves the wasp that has won a fight, and the one that has lost it. If a wasp of a strictly monogynous species loses a combat, if only through brief submission, it abandons the nest. If it is from a polygynous species, it remains at the nest, and becomes an auxiliary. When a wasp from a strictly monogynous species wins a combat, it maintains essentially the same behaviour towards other females. Its attacks are not stopped by the submissive posture of the other wasp. A wasp from a potentially polygynous species, on the other hand, assumes queen behaviour. It then adopts dominant behaviour towards other individuals, which replaces its initial aggressiveness.

We suggest that all these traits of behaviour express, according to the social situation, various consequences of only two "norms of reaction:" a strictly monogynous and a potentially polygynous norm of reaction. So the question of the selective origin of polygynous foundation becomes "what is the selective advantage of becoming a potentially polygynous female?"

Such a change from the question asked by West to ours can be said to be a postulate. But we state that:

This postulate leads to clearly different conditions for selection.
It seems to be reasonable or even, more likely than the alternative one.

AN EVOLUTIONARY MODEL

If, in a population, only some individuals possess the "potentially polygynous" norm of reaction, the achievement of a polygynous foun-
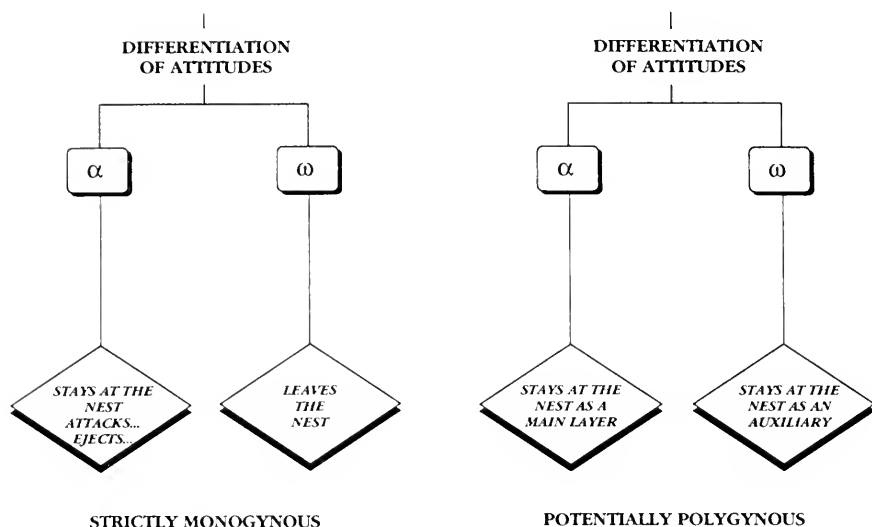
FIGURE 2. Differential forms of behaviour for both kinds of species after differentiation of attitudes.

dation does not, obviously, occur at random. It necessarily results from a behavioural screening: only females that possess this norm will actually be able to associate. This assumption leads to a model which has been called selection through affinity (or "pal selection").

Restricting the argument to digynous societies, it can be shown that the "potentially polygynous" norm will be selected if the following condition is fulfilled

$$P_{(f+j)} > P_{(f)} + P_{(j)}$$

with the same parameters as in West's formula.

Or, if one supposes that there is no difference in productivities of joiner and founder:

$$P_{(f+j)} > 2P_{(f)}$$

The main difference between this condition and that of West's model is the disappearance of parameter r expressing the degree of kinship. In fact, we can obtain this formula by making r equal to one in West's formula.

That is not surprising: parameter r expresses (according to Sewall Wright) the probability for two individuals to have a gene in common. The active assortment, in a model through affinity, ensures its value to be equal to one, concerning the gene responsible for associa-

tion, and this one only. Then, this model is a model of genetic related-ness: it is not a model of kin selection.

Consider a population (N) with a proportion (n) of potentially poly-gynous wasps and (1-n) strictly monogynous wasps. For simplicity sup-pose that:

- Each wasp has one encounter with another wasp, at the end of which it either founds alone, or enters a digynous society.
- The various possible encounters are a function of the proportions of the two types of females present in the parent population.
- Each wasp transmits its behavioural characteristic to its descendants. We are therefore referring here, metaphorically, to a "gene" for "poly-gynous potential." Genetic dominance and recombinations, which are symmetrical for the two opposing traits, can be ignored, as far as transmission of the character is concerned, and would merely delay the selective process without changing its character.

Admitting these assumptions, any encounter between a potentially polygynous wasp and one which is not, will have no genetic conse-quences in the following generation, in terms of the "polygynous trait" considered here. Association will not occur, and each wasp will found its own colony, producing its own genetically similar offspring.

The only events which will cause a change in trait frequencies are encounters between two potentially polygynous females: each such en-counter leads to a digynous society producing $P_{(f+j)}$ potentially poly-gynous females, and encounters between two nonpotentially polygynous females which will be followed by the foundation of two monogynous societies producing $2P_{(f)}$ nonpotentially polygynous descendants.

Thus we can observe n^2 encounters between two potentially poly-gynous females which produce $n^2 \times P_{(f+j)}$ potentially polygynous fe-males in the next generation. In the same way, $(1-n)^2$ encounters be-tween two strictly monogynous females produce $2P_{(f)} (1-n)^2$ strictly monogynous females in the next generation. Finally, $2n(1-n)$ encoun-ters between one potentially polygynous and one strictly monogynous female, result in $2n(1-n) P_{(f)}$ potentially polygynous and $2n(1-n) P_{(f)}$ strictly monogynous females. If frequencies in the following generation, of potentially polygynous and strictly monogynous wasps are, respec-tively, n' and n" we have:

$$n' = n^2 P_{(f+j)} + 2 n (1-n) P_{(f)}$$

$$n'' = 2 (1-n)^2 P_{(f)} + 2n (1-n) P_{(f)}$$

The potentially polygynous trait will be selected for if:

$$n' > n$$

$$n'' < (1-n)$$

These conditions can be written as:

$$n^2 \times P_{(f+j)} + 2\,n\,(1-n)\,P_{(f)} > n$$

$$2\,(1-n)^2 \times P_{(f)} + 2n\,(1-n)\,P_{(f)} < 1-n$$

Simplifying the two inequalities by n and $(1-n)$ respectively:

$$n \times P_{(f+j)} + 2\,(1-n)\,P_{(f)} > 1$$

$$2\,(1-n) \times P_{(f)} + 2n\,P_{(f)} < 1$$

Which stresses that:

$$n \times P_{(f+j)} + 2\,(1-n)\,P_{(f)} > 2\,(1-n)\,P_{(f)} + 2n\,P_{(f)}$$

or, simplifying again:

$$P_{(f+j)} > 2\,P_{(f)}$$

THE SELECTED TRAIT AND ITS BIOLOGICAL CHARACTERISTICS

The likelihood of the proposed model is bound to the relevance of a basic postulate; it concerns the functional unity of the norm of reaction that we consider as the target for selective processes. For that reason, we considered the behaviour of the females in both categories of species. According to our observations, several traits of behaviour do not differ from one category to the other one.

During winter, females can gather in overwintering groups. Dominance relationships seem to exist in these groups. Differentiation in individual behaviour during interactions is a part of species contact ritual. Individual wasps involved in confrontation during ovarian diapause show such behavioural differentiation as soon as they interact. Because of this, all members of hibernating groups are members of a hierarchy. It is true that overt dominance interactions are then rare, reflecting a low activity level. When seen, they indicate a typical linear hierarchy, with no associated differences in individual space use. Strong mutual attraction does, in fact, lead wintering individuals of several strictly monogynous Polistine species (*P. omissus, P. foederatus*) to associate in winter clusters, in a common shelter.

Two noteworthy events follow the resumption of reproductive activity. First, the pre-existing hierarchical relationships change and the newly established ones relate to individual endocrine conditions. Second, each wasp establishes an individual nesting area. Within it there is a restricted site, of specific functional significance (the "tache" = spot, *sensu* Deleurance, 1956) where activity is concentrated and nest construction begins.

The presence of the first structural nest components, and even more so of an incipient nest with several cells, has two effects. The nest is both attractive to and stimulating for any actively founding wasp. Indeed, a wasp which is in the prefoundation phase (*sensu* Deleurance, 1956) and which adopts a nest may immediately take up paper collection. The focal point (*tache*), and later the nest, becomes the site at which any reproductively active wasp tends to aggress others.

Aggressive interactions at this stage occur mainly between wasps of which one at least is effectively engaged in founding. The small nest is, at this stage, an attractive object which is actively defended against other females. Fights occur when two females direct their activities towards the same nest, and the individual that loses this fight becomes a subordinate. The differences shown in Figure 2 can explain for both kinds of species, the observations described by several authors.

In a strictly monogynous species, this common attraction by the nest leads to an usurpation (Yoshikawa, 1955) when the fight is won by the newcomer. The first occupant, then, leaves the nest and is attacked as soon as it comes back. As Makino and Aoki (1982) said "the dominant appears not to accept the subordinate rather than to manipulate her." According to concepts used by Schneirla (1965 a, b), a common approach to the nest is replaced, in the subordinate, by a withdrawal out of this territory.

In some species having a low aggressiveness, peculiar conditions can allow several females to cohabit, at least temporarily, at the same nest (pseudopolygyny). This has been recorded, although rarely, under natural conditions in normally monogynous species: *P. Jadwigae* (Yoshikawa, 1962; Kasuya, 1981); *P. chinensis antennalis* (Yamane, 1973); *P. biglumis* (Makino, 1982). The condition has also been induced experimentally: *P. jadwigae* (Yoshikawa, 1956); *P. foederatus* (Perna, Marino Piccioli, & Turillazi, 1978).

The common feature in these observations is the absence of behavioural differentiation of the kind classically observed in species which are more frequently polygynous. We attribute such pseudopolygyny to simple habituation, rare under natural conditions, induced by manipulations which favour the establishment of compound nests or which forcibly impose cohabitation in small cages under experimental conditions. A relatively low level of aggressiveness in the species concerned would favour such habituation. It is well known (Itô, 1985) that the degree of inter-individual agressiveness varies according to species.

In this view, each wasp would actually behave as a solitary, despite the effective cohabitation, ignoring other wasps as factors liable to affect its own reproductive behaviour. This has been emphasised by

Perna et al (1978). Here, female cohabitation would then be polygyny only from the observer's point of view.

Absence of behavioural differentiation would then mean that if a wasp is to express nesting behaviour, it has only two possibilities. The first would be to approach and occupy any nest territory it encounters. The second would be to avoid them and go away, even if a female is led to cohabit with its dominant, it seems to be unable to display an auxiliary behaviour. Reciprocally to the previously quoted sentence of Makino and Aoki, the subordinate tends to leave the nest rather than to become an auxiliary.

In a potentially polygynous species a departure of the subordinate may occur occasionally. More commonly, it is followed by division of labour which leads the subordinate to become an auxiliary. To understand the change involved, we must ask what this behaviour implies.

Pratte (1990b) has found that the members of a hierarchy in a trigynous *P. dominulus* society do not all have the same preferences for, or responses to attractive stimuli. Similar observations have been made for a postemergent monogynous society (Theraulaz, Pratte, & Gervet, 1990; Theraulaz, Gervet, Thon, & Pratte, 1991a; Theraulaz, Gervet, & Semenoff, b). Nests are particularly attractive to subordinate wasps when they contain larvae. These release a regurgitation reaction, and/or elicit food collection, but those wasps are less reactive to stimulations releasing egg laying or differential oophagy. On the other hand, the response of the dominant to young larvae is weaker, while its orientation towards empty cells (available for egg laying) and eggs is stronger. We summarise these facts by saying that dominance relationships affect a process of approach-withdrawal within the framework of reproductive behaviour.

Expressing a ritualised fight, they lead the winner (= dominant) to strengthen its attraction towards stimulations bound to the reproductive behaviour and the loser (= subordinate) to reduce its responsiveness to these stimulations.

The transition from strictly monogynous to potentially polygynous norms of reaction would concern how to manage these opposite trends. In the first case, approach and withdrawal take a geometrical meaning: stay at the nest (and expel other females) or leave it (and avoid the winner female). In the second case, they concern specific modes of investment of social space: turn to a layer behaviour (and only fight opponent females) or to a behaviour of auxiliary as previously described.

Such a change reminds us of the case, rather frequent, of transition from territorial to hierarchical behaviour. By the way, *P. canadensis* (West-Eberhard, 1986) is, to some extent, intermediate between strictly monogynous and potentially polygynous species: A

form of territory related dominance was described, in which a territorial queen actively suppresses aggressive behaviour of nestmates via physical approach and attack. This condition would support the proposed link between dominance and territoriality or, in other words, the effect of social rank on the use of social space in the nest.

Selection Through Affinity and Evolutionary Problems

At a theoretical level, a model of selection through affinity (or "pal selection") is more economical than the classical model of kin selection, but two remarks can be made:

We must show that a "pal directed" process is robust and can represent an evolutionarily stable strategy. In particular, any evolutionary trend is concerned with the problem of cheating, and we must ask if such a mechanism of active assortment can resist the income of a cheater.

It seems, according to several authors (Post & Jeanne, 1982; Gadagkar, 1985b; Gamboa, 1988; Gamboa, Reeve, & Pfennig, 1985), that some kin preference frequently exists for common association. This suggests that it led to some selective advantage, and thus, that some degree of kin selection did exist.

False-pals and cheaters.

Consider a population of "pals" accepting to become auxiliaries when they lose the fight of differentiation and becoming main layers when they win this fight. Suppose that a mutant "false pal" arises, which accepts help (that is, cooperates when dominant) but never gives it (defects when subordinate, and founds alone). In an environment of pals, "false-pals" will take the advantage and, thereby, eliminate all the "true pals" genes from the population. Then how can a "true pal" norm of reaction have been retained? We see only two possible answers to this question.

The first would argue that some structural constraint could have prevented the incoming of such a "false pal" behaviour. It may be that changes when dominant and subordinate would have consisted in the same ethological transition. Only a more accurate analysis of these norms of reaction will clarify this point.

The second one states that "false pal" behaviour is not an evolutionarily stable strategy. Since no mechanism can lead to an equilibrium between strains of "true pals" and "false pals," indeed the advantage of the "false pal" exists whatever the density of the "true pal." If the latter is eliminated, only monogynous foundation can occur and the "false pal" strategy no longer has any selective advantage, or can even be counterselected.

A "false pal" strategy can be stable only if a mechanism exists that leads to an equilibrium between "true pal" and "false pal" genes.

That is possible if "false pals" are, at the same time, "lazy," i.e., unable to found a new colony when alone. Then the scarcity of "true pals" leads to a rather drastic situation for false pals, while the few remaining "true pals" are able to found new colonies.

Such a regulatory mechanism is more easily involved if a genetic isolation between the two strains allows a "true pal" colony to lay only "true pal" offspring. Then an equilibrium can be established at a level that depends on the ability of each strain to promote its own strategy. In fact, such a "lazy false pal" behaviour exists; it is the one of the social parasites belonging to the Sulcopolistes genus. Thus, such a scenario would explain the origin of social parasitism among paper wasps.

Pal Selection and Kin Selection

A process of kin selection for polygynous foundation can only occur if two (or even three) factors are involved: kin preference for association, ability for the subordinate to become an auxiliary, and ability for the dominant to accept its subordinate in the nest. A "pal selection" process involves only one change, which is the previously quoted change of norm of reaction. It is apparently more economical; but, at the same time, it involves one constraint: the existence of norms of reaction as described. Similarly, it suggests a grid for study of social reactions to polygyny. On the other hand, two differences between the models are relevant for evolution:

First, a "pal" directed process is faster than a "kin" directed process, since it can be considered (for evolution) as a "kin" process in which r is equal to 1.

Second, its genetic effects are not the same: only the gene of the auxiliary which is responsible for association is replicated in the next generation, while the other ones are counterselected. This second difference leads to several consequences.

Within the genome of the auxiliary, this fact gives a selective advantage to every mutation which, at other loci, could weaken the effects of the "pal" allele. But, this is true only if ecological conditions allow a monogynic foundation to give offspring.

A polygynous foundation obtained by a "pal" directed evolutionary process gives the best conditions for a subsequent selection of any "kin preference" gene which would have arisen at another locus in the genome of the joiner that becomes subordinate.

Thus, we can suppose that the evolutive appearance of polygyny in paper-wasps—or, more generally, in a semi-social group implying kin preference—would have involved two successive steps.

A process of pal selection, leading to groups of females possessing the main characteristics of polygynous societies, as described. In par-

ticular, this is compatible with Carpenter's (1989) scenario stating that a stage of casteless nest sharing may not have occurred.

The incoming of a kin preference bound to a new selective process having occurred after the appearance of the polygynous group.

Possible existence of these two steps suggest that the different hypotheses (parasocial group: Lin & Michener, 1972; polygynous family: West-Eberhard, 1978) point to possible scenarios but not to necessary prerequisites for a subsequent evolutionary trend to eusociality in insects.

CONCLUSION

Even, if, by nature, an evolutionary model is to remain rather conjectural, we believe that the postulated selective process, discussed here under the term affinity selection or pal selection is plausible, given details of behaviour we have actually observed in Polistines. We would also stress that it is quite compatible with Hamilton's model (1964). We further note that it does not conflict with the kin selection model, but does appeal to some additional considerations, as illustrated by three points:

It is more parsimonious in its requirements than kin selection. However, it is clear that if wasps associate because they carry a same allele, the probability of affinity is greater for related wasps. This the more so where the frequency of the trait is still low in a population as a whole.

It is not open to Maynard Smith's (1976) objection (previously quoted), because expression of a potentially polygynous behaviour and choice of individual helped are not different traits of behaviour but simply different consequences of the same trait. The expression of the behaviour will itself automatically lead to assortment in a population of wasps possessing the trait. Here the model avoids the previously quoted difficulty in the Green Beard Model.

It leads to selection for genes associated with polygynous behaviour, without directly affecting other genome components, whereas a model involving kin relationships would tend, at least in the short-term, to facilitate transmission of genes frequent in the parent strain as well.

The implications of this fact for genetic diversity remain obscure in the case of a polygynous society, but these implications could become appreciable for an analogous model which considers assortive mating. Rushton et al. (1984, 1988) referring to a very different biological material (*Homo sapiens*), considered that selection based on genetic affinity could offer protection against excessive inbreeding. Optimal fitness, they write, ". . . consists in selecting a mate who is genetically similar but not actually a relative."

Beyond the problem treated here at the level of the Polistines, we would raise a problem central to the study of evolution, and more particularly relating to the evolution of behaviour. This is identification of the units of selection.

Gayon (1989) and Gliddon and Gouyon (1989) commented on confusion between two distinct problems. The first concerns the biological units between which selection operates (units of selection) and the second the nature of the unitary traits retained in a population by selection (units for selection).

The first has often been treated by ethologists and evolutionary theoreticians. The concepts of individual selection, group selection, kin selection, and interdemic selection have generated detailed mathematical models. It is now possible to consider both the ecological conditions and the behaviour which are required if they are to be valid.

In contrast, we have stressed the second of these problems, the definition of the selected trait. We believe that the question is essential to ethology: the most conspicuous feature of a behavioural trait, for the observer is not necessarily the most pertinent in terms of selection. We claim that one cannot state a selective process without having previously said what has been selected. Only by this manner will ethological analysis and selective models be able to enlighten each other. Then, it will be possible both to more accurately describe the selective origin of actual behavioural traits and to find how the behaviour can organize the network of interactions within a population and, thereby, direct its own evolution.

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MATERNAL BEHAVIOUR IN DOMESTIC HENS (*Gallus gallus domesticus*): CUES FROM CHICKS AND MAINTENANCE OF MATERNAL RESPONSIVENESS

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ABSTRACT: Maternal responsiveness in adult hens was measured by studying their rates of vocalization over a period of 12 days. Four groups of hens were compared: one group was isolated both visually and tactually from chicks; two other groups were exposed either to visual cues or to tactile cues originating from chicks, and in the last group, hens received both types of cues. Visual or tactile cues alone induced similar levels of maternal responsiveness but simultaneous presentation of both types of cues induced maximum responsiveness.

RESUME: Grâce à l'analyse des vocalisations émises, la réactivité maternelle de poules adultes induites a été estimée pendant une période de 12 jours. On a ainsi comparé 4 groupes de poules: certaines sont isolées visuellement et tactilement des jeunes, d'autres sont exposées soit aux stimulations visuelles soit aux stimulations tactiles émanant des petits, tandis que dans le dernier groupe, les poules reçoivent à la fois les deux types de stimulations. Il apparait que la présence des stimulations visuelles ou tactiles est nécessaire pour que la réactivité maternelle se perpétue. Ces stimulations visuelles ou tactiles seules permettent un maintien équivalent de la réactivité maternelle tandis que la réactivité maximale est observée chez les animaux qui reçoivent les deux types de stimulations.

INTRODUCTION

In domestic hens (*Gallus gallus domesticus*), it is possible to induce maternal behaviour typical of the species by confining a hen with chicks (Burrows & Byerly, 1938; Collias, 1950; Ramsay, 1953; Maier, 1963; Richard-Yris, Garnier, & Leboucher, 1983). At least two physiological changes also coincide with this expression of maternal behaviour: egg production ceases in hens that were laying and plasma concentrations of steroid gonadal hormones decline in nonlay-

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275

ing as well as in laying hens (Richard-Yris et al., 1983; Richard-Yris, Leboucher, Chadwick, & Garnier, 1987 a; Richard-Yris, Leboucher, William, & Garnier, 1987 b). Visual, tactile and/or auditory cues originating from chicks could be the cause of this process. Several studies suggest that tactile stimuli are predominant.

Maternal behaviour has been shown to be induced more easily in hens exposed to chicks during the dark (when tactile stimulation is likely) than in hens exposed to chicks during the light phase (when visual contacts are predominant) (Richard-Yris & Leboucher, 1987 a). Similar results presented by Maier (1963) showed that hens that could only hear and see chicks took much longer to become maternal than hens that could also touch chicks with their breasts. Finally, Opel and Proudman (1988) showed that in incubating turkeys, tactile stimulation from poults was essential to induce a decrease in plasma prolactin levels. Furthermore, visual and auditory cues played only a minor role in this process.

According to McBride, Parer, and Foenander (1969), chicks begin to display independence as late as 5-6 weeks of age and become very independent by the age of 12-14 weeks. Wood-Gush (1971) found that family severence in domestic fowl occurs at the age of 6 to 8 weeks. Therefore, hens may be said to perform maternal activities with chicks for approximately 2 months. We believe that the presence of chicks is necessary to maintain this maternal responsiveness (Richard-Yris et al., 1983; Richard-Yris & Leboucher, 1986 a).

In natural broods, relationships between hen and chicks change qualitatively and quantitatively with the age of chicks. Particularly in feral hens, brooding activity decreases as age of chicks increases (Sherry, 1981). Similar changes were found after experimental induction of parental behaviour by confining hens with chicks (Richard-Yris & Leboucher, 1986 b). As chicks grow, they gradually become thermally independent and make physical contact with their mother less and less frequently. However, even after these tactile stimulations disappear, hens continue to care for their young by uttering typical maternal calls (personal observation). Therefore, we expect maternal behaviour to be maintained by visual or auditory stimulations as well as by tactile stimulation from the chicks. Nevertheless, experimental research carried out by Maier (1963) appears to attribute the maintenance of maternal responsiveness only to the possibility of physical contact between hen and chicks.

The aim of this paper is to analyse in detail the effect of the visual and tactile stimulation hens receive from chicks on the maintenance of maternal responsiveness. The strong relationship between a hen's maternal state and her ability to utter maternal calls (i.e., clucks, food calls, roosting calls) in reply to chick distress calls is well documented (Collias, 1950; Ramsay, 1953; Richard-Yris et al., 1983;

Richard-Yris & Leboucher, 1986 a). Vocalizations by hens were used therefore to evaluate maternal responsiveness.

MATERIAL AND METHODS

Animals and Maintenance

We observed 32 adult Vedette J.V.15 hens (a heavy dwarf strain) obtained from an industrial centre (Couvoir de la Vilaine). Each hen was placed individually in a wire-mesh cage (100 × 70 × 60 cm) with opaque lateral partitions and provided with a wooden nest-box (40 × 30 × 40 cm). They were visually, though not auditorily, isolated from the others. Temperature was maintained at 22 ± 2°C under a fixed 12 h light-dark cycle.

Pre-Experimental Treatment

Maternal response was induced by following a conventional method (induction) in which each hen was maintained with two newly hatched chicks (Richard-Yris & Leboucher, 1987 c). After 7 days, the two foster chicks were replaced during the dark phase by two newly-hatched chicks.

Experimental Groups

On the eighth day after the beginning of induction, the experiment was begun (i.e., Day 0). At the start of the dark phase, the hens were assigned to one of four experimental groups.

None of the animals were acoustically isolated and all could hear chick vocalizations from chicks in their own or in neighbouring cages.

Group A (n = 8): "Isolated hens." At the beginning of the experiment, chicks were removed from the cages, and subsequently, these hens had neither physical nor visual contact with chicks.

Group B (n = 8): "Visual hens." Each morning for 12 days, two chicks were placed in a wire cage immediately in front of the hen's cage. They had food and water *ad libitum*. Every evening, the chicks were placed in another heated room so that the hens in this group did not have direct access to chicks during the dark phase.

Group C (n = 8): "Tactile hens." Each evening, two chicks were placed in the cage of each hen when lights were switched off. The chicks were removed every morning, 15 min before the lights were switched on. These hens did not have direct access to chicks during the daylight period.

Group D (n = 8): "Visual and tactile hens." These hens could see chicks during the day (like Group B hens) and they could touch chicks during the night (like Group C hens).

Vocalizations by Hens (Tape Presentations)

On Days 0, 1, 2, 3, 4, 6, 8, 10 and 12, counts of each hen's vocalizations in response to a 2 min tape of chick distress calls played were made in a dark room (210 × 210 × 280 cm).

The number of the following calls were noted as they occurred during the observation period.

1. clucks
2. food calls
3. roosting calls (purring calls)
4. laying calls, nonmaternal calls uttered mainly by hens during periods of important ovarian activity
5. other vocalizations emitted during the observations such as alarm calls and tension calls. These were counted and included in the total of vocalizations, but were not analysed separately.

The first three calls are described as attraction calls (i.e., maternal calls). For detailed descriptions of these vocalizations see Baeumer (1962), Konishi (1963), Guyomarc'h (1974), Collias (1987). The different vocalizations were counted directly as the observer heard them. At the same time, these vocalizations were tape recorded and counted again, after the observation.

The following measures were analysed in detail:

1. The total number of maternal calls (clucks, food calls, roosting calls) uttered by each hen during each observation. This count indicates general maternal responsiveness.
2. The number of clucks.
3. The number of food calls.
4. The number of laying calls.

Roosting calls were not analysed in detail as these calls were emitted rarely and by only a few hens during the entire experiment.

In addition, the proportions of each different category of vocalization in relation to the total number of vocalizations were converted to percentages and analysed. For example, if a hen uttered 30 clucks during an observation out of a total of 40 calls, the percentage of clucks for this hen was 75%. If a hen did not utter any vocalizations, by convention, the percentage was recorded as 0.

Chick Test

On Day 12 of the experiment, each hen was presented with two unknown, group-raised chicks the same age as her own. These tests were performed in the same room, but with the lights on.

All behavioural activities and vocalizations of the hen were recorded.

Statistical Analyses

Data were analysed using analysis of variance with models based on repeated measurement designs and if appropriate ($p < .05$), a further post hoc analysis was carried out using the protected least significant difference (PLSD) Fisher test (Winer, 1971).

RESULTS

On Day 0, all hens showed typical maternal responses, that is, they emitted many maternal calls, especially clucks during tape presentations. However, later the hens showed different responses, depending upon their experimental treatment.

Tape Presentations

Variations in the number of vocalizations over time. In Groups A, B, and C the rates of general maternal responsiveness (i.e., total number of maternal calls) showed a significant decline during the experimental period (Figure 1). This trend did not occur in Group D hens which received both visual and tactile stimulation from chicks.

A decline in the quantity of clucks, the main maternal call, was observed in all the groups during the experiment. The quantity of food calls did not vary significantly with time in Groups B, C, and D that received visual or tactile cues, or both, from chicks, but decreased significantly and disappeared completely after Day 6 in hens isolated from chicks (Group A). In this group, the number of laying calls increased significantly after mother and young had been separated.

Intergroup comparisons. Vocalizations showed significant differences among the four experimental groups by Day 6 (significant group effect, ANOVA, $p < .05$).

On the basis of general maternal responsiveness and the number of clucks, we were able to divide the animals into three well separated groups (Figure 1: 1 & 2): Group D hens showed the highest values and hens of both Group B and Group C, which never differed significantly one from each other, produced intermediate values; Group A showed the lowest scores ($D > B, C > A$, PLSD Fisher test, $p < .05$).

Comparative analysis of the number of food calls (Figure 1: 3) revealed a similar situation as Group D hens again showed the highest scores, and Group A hens the lowest ones. However, in this case
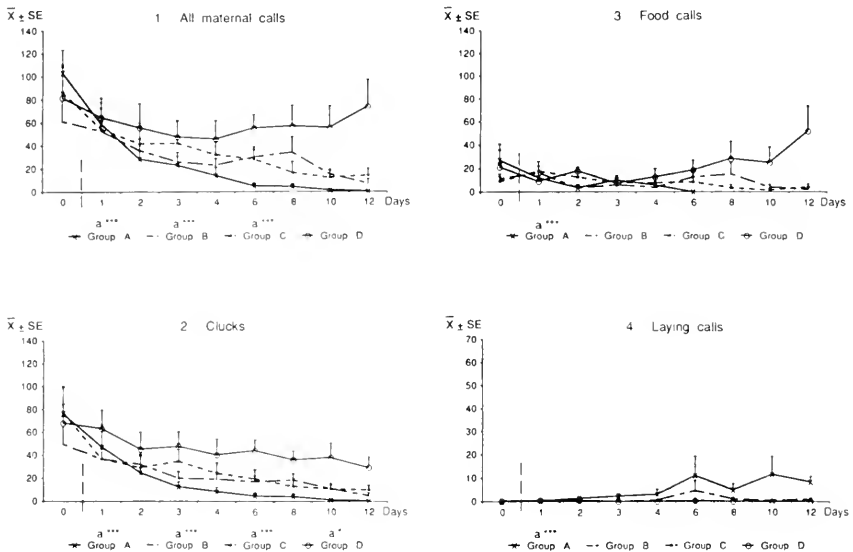
FIGURE 1. **Vocalizations emitted by hens in experimental group during successive tape tests.** Group A : isolated hens; Group B : visual hens; Group C : tactile hens; Group D : visual and tactile hens. a: indicate a significant time effect (Anova). *: $p < .05$; ***: $p < .0001$

the differences between the data for Groups A and C were never statistically significant and differences among the data for Groups D and B and for Groups D and C reached the .05 significant level only after Day 8.

Finally, Group A hens (deprived of visual and tactile cues) yielded the highest scores of laying calls as early as Day 3, whereas in Groups B, C and D the number of laying calls remained at an extremely low level (Figure 1: 4) (A > B, C, D, PLSD Fisher test, $p < .05$).

When the relative proportions of the different vocalizations in relation to the total number of vocalizations (maternall calls + laying calls + other vocalizations) uttered by each hen, for each test day, were taken into consideration (Figure 2), the hens can be clearly divided into two separate sets. Significant differences appeared between these two sets from Day 3 (significant group effect, ANOVA, $p < .05$) with Group A > Groups B, C and D for the percentage of laying calls and Groups B, C and D > Group A for the percentage of maternal calls (PLSD Fisher test, $p < .05$). In the first set of hens, the relative proportion of maternal calls declined rapidly, whereas the relative proportion of laying calls increased (Group A hens). In the second set
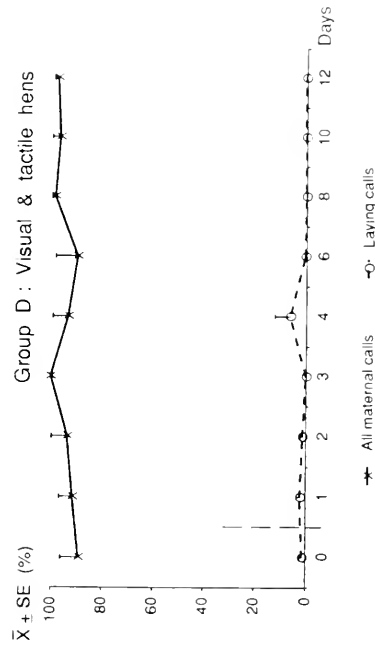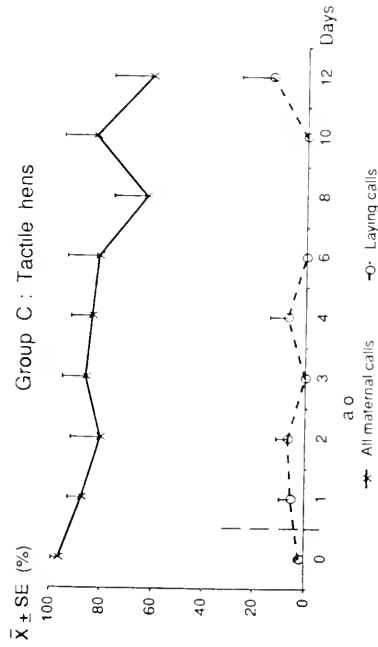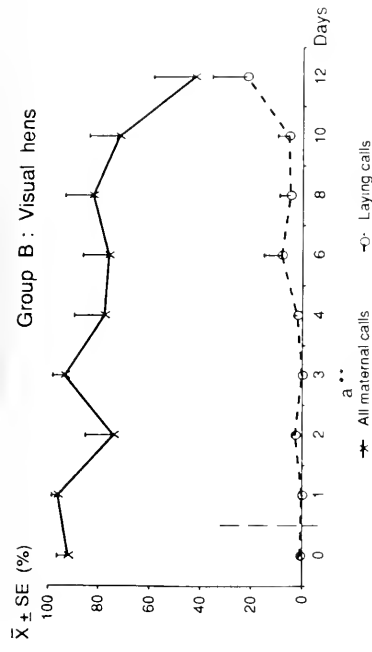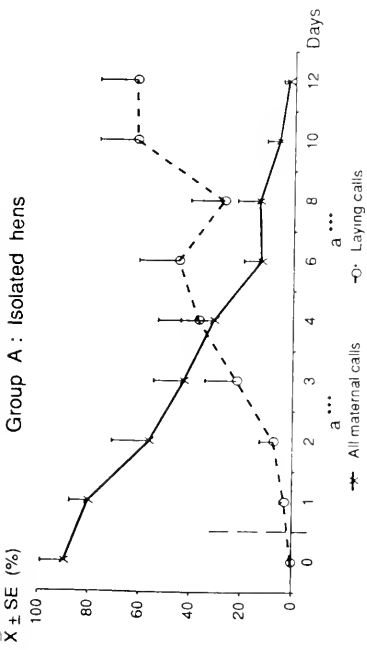
FIGURE 2. Variations of all maternal vocalizations and of laying calls during tape tests (in percent of the total of all vocalizations recorded) for each experimental group. A : isolated hens; B : visual hens; C : tactile hens; D : visual and tactile hens. a: indicate a significant time effect (Anova). o: p < .10; **: p < .001; ***: p < .0001

of hens, the relative proportion of maternal calls remained high for the entire duration of the experiment except a slight decline on Day 12 for Groups B and C while the relative proportion of laying calls remained low (Group B, C, and D hens).

When data for Groups B, C, and D were analysed in more detail, differences between these three groups were revealed. In Group D, the proportion of maternal calls remained constantly at a high level (approximately 90%), whereas in Groups B and C this proportion tended to decline slightly, particularly in Group B between Days 10 and 12 (significant time effect, ANOVA, $p < .05$).

The general maternal responsiveness for the two partially deprived groups of hens (Groups B and C) differed significantly from that for Group D hens only on Day 12 (PLSD Fisher test, $p, < .05$), whereas no significant differences appeared concerning the proportion of clucks. The difference between maternal responsiveness scores on Day 12 was correlated to the greater participation of food calls in vocalizations by Group D hens.

Chick Test

All vocal criteria differed significantly (ANOVA, $p < .001$) among the four experimental groups during direct exposure of each hen to two unknown chicks on Day 12. These tests revealed important differences between the behaviour of Group A hens and that of hens in the other groups.

Group A hens were characterized by a very low level of maternal responsiveness: only 1 hen uttered any maternal vocalizations, 6 uttered laying calls, and 4 out of 8 hens pecked at the chicks (Table 1). In contrast, all hens in the other groups immediately accepted the chicks that were presented to them, and none attacked a chick. Groups B, C, and D hens did not differ significantly concerning clucks (absolute number or percentage). Group C hens uttered more food calls than did hens of the other two groups, but only the difference with Group B hens is significant. Consequently, on the whole, Group B hens uttered a lower number of maternal calls than Groups C and D hens did.

DISCUSSION

Placing hens in situations that resulted in various levels of deprivation of stimuli from their chicks revealed that the different types of deprivation did not all have the same effects on maternal responsiveness. Group A hens that could neither see their chicks nor make contact with them lost their ability to respond maternally to chick calls

TABLE 1
Vocalizations (X ± SEM) and Pecks During Chick Presentation Tests

Groups	A "Isolated" hens n = 8	B "Visual" hens n = 8	C "Tactile" hens n = 8	D "Vis. & Tact." hens n = 8
Pecks	(50)	(0)	(0)	(0)
Clucks		a	a	a
X ± SEM	0.75 ± 0.75	14.13 ± 5.15	24.38 ± 8.8	37.25 ± 10.37
	(12.5)	(87.5)	(100)	(100)
Food calls		a	a, b	a
X ± SEM	4.75 ± 4.75	17 ± 7.63	73.38 ± 13.71	37.75 ± 10.85
	(12.5)	(62.5)	(100)	(100)
Roosting calls		a	a	a
X ± SEM	0.5 ± 0.5	0.5 ± 0.5	0.37 ± 0.37	0.13 ± 0.13
	(12.5)	(12.5)	(12.5)	(12.5)
All maternal calls		a	a, b	a, b
X ± SEM	6 ± 6	31.63 ± 11.73	98.13 ± 15.81	75.13 ± 13.28
	(12.5)	(87.5)	(100)	(100)
Laying calls		a	a	a
X ± SEM	4.5 ± 1.52	0.25 ± 0.25	0.13 ± 0.13	0.63 ± 0.63
	(75)	(12.5)	(12.5)	(12.5)

Note. Number in brackets indicate the percentage of hens performing the corresponding behaviour. a,b: significantly different from Group A,B respectively (P.L.S.D. Fisher test, p <.05).

quite rapidly. On Day 6 none uttered food calls any longer and only one Group A hen was still able to cluck a little on Day 10. In addition, half of them behaved aggressively towards the chicks on Day 12. Therefore, it seems that perception of chick calls alone (it must be remembered that Group A hens could perceive chick calls from neighbouring cages) is not sufficient to maintain maternal responsiveness for some time. Although these experiments bring no proof either way of the possible role played by chick calls in maintaining responsiveness for shorter periods, a previous experiment (Richard-Yris & Leboucher, 1986 a) showed that total removal of chicks was followed by a very rapid loss (in 5 days) of vocal maternal responsiveness in hens. Nevertheless, further experiments would be necessary to investigate this relationship. While Group A hens gradually lost their maternal characteristics during the experiment, other characteristics (reddening of crest, utterance of laying calls) indicating that ovarian activity was increasing (Richard-Yris & Leboucher, 1986 a) could be observed. In the same way, under natural conditions, total removal of chicks allowed hens to resume laying rapidly (Savory, 1979; Sharp, Scanes, Williams, Harvey, & Chadwick, 1979).

In contrast, Group D hens, which could see the chicks during the day and have tactile contacts with them at night, showed strong maternal responsiveness during the entire experiment. They emitted many clucks and food calls in reply to chick calls and accepted new chicks immediately when they were presented on Day 12. Therefore, it seems that the possibility to interact directly (contact, following responses, etc) with chicks during the day, as hens normally do, is not absolutely necessary to maintain efficacious maternal responsiveness.

When hens could receive only visual cues (Group B) or only tactile cues (Group C), the data presented intermediate values. These hens remained maternal as they did not emit laying calls, but they continued to cluck and emit food calls and they accepted the new chicks on Day 12. However, during the tape presentations, they produced less maternal calls than Group D hens did, thus indicating a lower level of maternal arousal than Group D hens.

These results do not allow us to make any statement about the superiority of one sensory channel over the other, because the vocalizations during the tape tests revealed no significant differences between Groups B and C. The only difference we could find occurred when hens were confronted directly with chicks on Day 12. In this case Group C hens uttered more food calls than did Group B hens (and also at a lower level than did Group D hens). It is well known that visual stimulations from chicks play a major part in the production of food calls by maternal hens (Sherry, 1977). This fact can explain that, on the whole, maternal hens produced more food calls during chick tests, when they could see chicks, than during tape pres-

entations, when they could only hear them (Richard-Yris & Leboucher, 1987 b). The long period of deprivation of visual contact with chicks that Group C hens underwent could possibly have increased the stimulating effect of seeing chicks during the test. However, there is another plausible hypothesis: Groups B and D hens that have seen chicks during the daytime never experienced complete approach responses following food calls as they were separated from chicks. This fact could explain why hens subsequently emitted less food calls during the chick test: nevertheless, further experimentation is needed to test these hypotheses.

Our results allow us to stress the following three important points:

First, auditory stimulations alone are not sufficient to maintain a significant level of maternal responsiveness over a period of 12 days.

Second, at least for the period studied, visual cues alone and tactile cues alone were sufficient to maintain a similar level of maternal responsiveness.

Third, the more stimulations received by the hens from the chicks, the higher the level at which maternal responsiveness was maintained (comparisons between Group D and each of Groups B and C).

Our data, therefore, indicate that in hens as in mammals (see review in Harper, 1981) the general concept of multisensory control of maternal behaviour seems to be substantiated.

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ACKNOWLEDGMENT OF REVIEWERS

Thomas M. Alloway
Marc Bekoff
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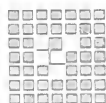
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